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ÅSA STAM

GROWTH AND RESILIENCE OF NON-VASCULAR EPIPHYTES IN THE TAITA HILLS, KENYA

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Faculty of Biological and Environmental Sciences
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Åsa Stam

ACADEMIC DISSERTATION

To be presented for public discussion with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki, in hall 6, Metsätalo, on the 11th of September 2020, at 12 o´clock.

Helsinki 2020

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Cover photo: Leafy liverwort in the Taita Hills, Kenya (Jouko Rikkinen).

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Abstract

Non-vascular epiphytes (bryophytes, lichens) play an important ecological role in tropical montane cloud forests. Bryophytes and lichens influence hydrological conditions in forest canopies by intercepting large amounts of water and, through evapotranspiration, helping to maintain high humidity long after precipitation has ceased.

Despite their obvious ecological importance, also for insects and other animals, few experimental studies on their ecology have yet been done in the tropics. For the remaining cloud forests in East Africa, basic information on biomass distribution and growth potential is urgently needed to better understand the various roles of non-vascular epiphytes in these montane ecosystems.

The aim of this thesis was to study responses of tropical non-vascular epiphytes to environmental factors. Because of their sensitivity to atmospheric conditions, changes in the forest environment can effect epiphytes in many ways. I studied such effects in the montane forests of Taita Hills, Kenya. I analyzed epiphyte growth and resilience experimentally with the help of pendant transplants and studied epiphyte colonization of artificial substrates in different forest environments.

The transplant studies provided a wealth of data on the ecology of non-vascular epiphytes. This included novel information on the growth responses of several epiphytic bryophyte and lichen species and their relations to environmental factors. Probable effect of climate change on the non-vascular epiphytes were simulated by comparing transplant performance in moist upper montane forests and drier lower montane forests, respectively. Results also indicated that the absence of many non-vascular epiphytes from exotic tree plantations more likely reflects the lack of suitable substrates than differences in forest microclimate.

We developed a new method for documenting epiphyte colonization with the help of plastic nets. The results revealed consistent differences in epiphyte cover, biomass and community composition between different types of forests. Finally, floristic observations contributed to overall knowledge of epiphyte diversity in the study area and led to the discovery of many epiphytic species that were new for the Taita Hills region.

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Contents

List of original publications

This thesis is based on the following publications:

I	Stam, Å., Enroth, J., Malombe, I., Pellikka, P. and Rikkinen, J. 2017. Experimental transplants reveal strong environmental effects on the growth of non-vascular epiphytes in Afromontane forests. *Biotropica* 49: 862–870.
II	Stam, Å., Anttila, J., Pellikka, P. and Rikkinen, J. 2020. Sensitivity of tropical pendant bryophytes: results from a translocation experiment along an elevation gradient. *Annales Botanici Fennici* 57: 71–81.
III	Stam, Å., He, X., Kaasalainen, U., Toivonen, M., Enroth, J., Räsänen, M. and Rikkinen, J. 2020. Epiphyte colonisation of fog nets in montane forests of the Taita Hills, Kenya. *Annales Botanici Fennici* 57: 227–238.
IV	Enroth, J., Pócs, T., He, X., Nyqvist, P., Stam, Å., Malombe, I. and Rikkinen, J. 2019. An annotated checklist of the bryophytes of Taita Hills region, Kenya. *Acta Musei Silesiae*, *Scientiae Naturales* 68: 53–66.

The publications are referred to in the text by their roman numerals.

Authors contributions to the publications:

I	JR introduced the idea and ÅS and JR designed the study. The field work was performed by ÅS. Data analyses were performed by ÅS and JR. ÅS wrote the paper as main author together with JR. All authors commented.
II	ÅS and JR designed the study. The field work was performed by ÅS. Data analyses were performed by JA. ÅS wrote the paper as main author together with JA and JR. ÅS was the corresponding author. All authors commented.
III	ÅS and JR designed the study and collected the material. MT and ÅS documented and analyzed the material. XH, UK and JE identified the species. Data analyses were performed by MR and JR. ÅS wrote the paper as main author together with XH, UK, MT, MR and JR. ÅS was the corresponding author. All authors commented.
IV	JE, TP, XH and PN identified the species. ÅS and JR collected the material. JE wrote the paper as main author together with all authors. All authors commented.

Summary

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1. Introduction

Tropical mountain cloud forests (TMCFs) occur at relatively high altitudes (normally 1200–3000 m asl) in the tropics. The forests are characterized by high atmospheric humidity and experience regular cloud immersion and frequent rain events. They typically support a high diversity and biomass of epiphytes. The reason for the high epiphyte biomass is the constantly moist environment and the lack of night frosts, which lead to a year-round growth of the plants (Gradstein 2008). The nearly constantly saturated air especially benefits non-vascular epiphytes that can absorb water directly from the atmosphere. The abundance of epiphytic bryophytes and lichens tends to increase with increasing elevation and major changes in epiphyte community composition are also typically observed along elevation gradients (Gradstein 2008; Jácome *et al.* 2011; Wagner *et al.* 2012).

The spatial distribution of TMCFs is restricted as the altitude band of cloud formation is limited, which makes the forests sensitive to climatic changes (Foster, 2001). Global warming may significantly reduce areas that have potential to support cloud forests and, as pointed out by Still *et al.* (1999), the forests that presently occupy summits of relatively low mountains are at highest risk.

Bryophytes are plants that lack true vascular tissue and vascularized organs (roots, stems, and leaves). They include the mosses (Bryophyta), liverworts (Marchantiophyta) and hornworts (Anthocerotophyta). Lichens are stable symbioses between heterotrophic fungi (mycobionts) and photosynthetic algae and/or cyanobacteria (photobionts). Bryophytes and lichens commonly co-occur in the specific microhabitats and are often analyzed together in ecological studies (Barkman 1958; Gradstein 1992). Epiphytic bryophytes and lichens are important components of biodiversity in tropical montane cloud forests (Gradstein 1992; Bruijnzeel *et al.* 2010; Tuba *et al.* 2011; Metcalfe & Ahlstrand 2019). Nonvascular epiphytes can grow abundantly on tree trunks and branches, but also on thin twigs and even on leaf surfaces (Pócs 1982; Gradstein 1992).

Both bryophytes and lichens absorb water and nutrients through their entire surface and are therefore easily influenced by the atmospheric conditions (Porada *et al.* 2018). On the other hand, many of them are poikilohydric and can tolerate repeated wetting and drying (e.g. Tuba 2011; Metcalfe & Ahlstrand 2019). Nonvascular epiphytes absorb water either directly from rain or stemflow, but also from fog and dew. Several authors have emphasized that water uptake from fog is of great importance to cloud forest epiphytes (e.g. Grubb & Whitmore 1966; Pócs 1980) and to cloud forest ecosystems both locally and globally (Porada *et al.* 2018). Their ability to effectively capture moisture influences the hydrological conditions of forest canopies through interception and temporary storage of large amounts of water and, by subsequent evapotranspiration which helps to maintain high atmospheric humidity also after the precipitation or fog event has passed (Bruijnzeel *et al.* 2010; Van Stan & Pypker 2015; Porada *et al.* 2018).

Because non-vascular epiphytes do not have direct access to resources on the ground, they are vulnerable to changes in their atmospheric surrounding and can be the first organisms to be affected by a disturbance in the forest (Slack 2011; Gotsch *et al.* 2016). Many nonvascular epiphyte species are threatened by habitat destruction, forest clearing, and air pollution. Such species cannot tolerate abrupt environmental changes and may easily disappear for example due to logging (Alvarenga *et al.* 2009; Sporn *et al.* 2010; Benítes *et al.* 2012; Király *et al.* 2013). Some nonvascular epiphytes are extremely sensitive to all types of disturbance and climate change represents an obvious threat to their existence (Zotz & Bader 2009; Rikkinen 2015; Zartman *et al.* 2015, He *et al.* 2016). The warming and drying climate may have a severe impact on epiphytic bryophytes of tropical upper montane forests as many of them are desiccation intolerant (e.g. Nadkarni 2010; Pardow & Lakatos 2013). A reduction in epiphyte diversity and biomass may have cascade effects on many other species, including invertebrates and birds (O´Neill

2000; Vitt & Wieder 2009; Slack 2011). A reduction of epiphyte cover may also lead to greater surface runoff and nutrient leaching, which in turn leads to biologically impoverished and less resilient ecosystems (Gotsch *et al.* 2016). However, compared to other plants like trees, crops and grasses, the potential effect of climate change on bryophytes has not received that much attention (Tuba 2011; He *et al.* 2016).

Non-vascular epiphytes can potentially be used as biosensors to predict environmental changes both at the global level (climate change) and more locally (environmental changes due to atmospheric pollution, forestry etc.). Epiphyte transplant studies offer a practical way of documenting growth patterns and differences in the growth responses of different epiphyte species (McCune *et al.* 1996; Sillett & McCune 1998; Larson *et al.* 2012). Transplantation of epiphytic lichens and bryophytes have been used to investigate the relations of growth to habitat type (e.g. Muir *et al.* 2006; Song *et al.* 2012), effects of air pollution (e.g. Bignal *et al.* 2008; Slack 2011), and as a method for *in situ* conservation (e.g. Gunnarsson & Söderström 2007). However, almost all transplantation studies have so far been done in cool or temperate regions of the world with very limited comparable data from tropical environments (Nadkarni 2000; Nadkarni & Solano 2002; Jácome 2011).

2. Aim of the thesis

The main aim of this thesis was to produce new information of non-vascular epiphytes in tropical montane cloud forests in East Africa. One central goal was to create and test methods for monitoring the growth of epiphytic bryophytes in the tropics.

In Articles I and II we developed and tested a new method for transplanting tropical epiphytes, especially pendant mosses, and analyze how different bryophyte species respond to growth conditions under the forest canopy.

In Article III we developed and tested a new method for studying epiphyte establishment and studied the effects of environmental conditions on the colonization success of different groups of non-vascular epiphytes.

In Article IV we produced an annotated checklist of bryophytes in Taita Hills region based both on our own collections and previous literature.

3. Material and methods

Study area

The Taita Hills of southeastern Kenya (3°25´S, 38°20´E, Figure 1) form the northernmost extension of the Eastern Arc Mountains which together with the neighboring Costal Forests represent a hot spot of global biodiversity (Myers *et al.* 2000; Burgess *et al.* 2007). Despite their relatively small area, the Taita Hills support high biodiversity and an exceptional level of endemism (Rogo & Oguge 2000; Pellikka *et al.* 2009; Aerts *et al.* 2010, Pellikka *et al.* 2018). Taita Hills are surrounded by dry plains which lay at 500–600 meters above sea level, while Vuria, the highest peak of Taita Hills, reaches up to 2208 m asl.

Taita Hills are affected by the trade winds from Indian Ocean which bring warm moist air, which is uplifted when reaching the mountain slopes and condenses into clouds and frequent fog around the highest peaks (Pellikka *et al.* 2009; Räsänen *et al.* 2018). The region experiences long rains between March and May and short rains between November and December, with pronounced dry seasons in between, but the highest elevations receive some rainfall throughout the year (Table 1).

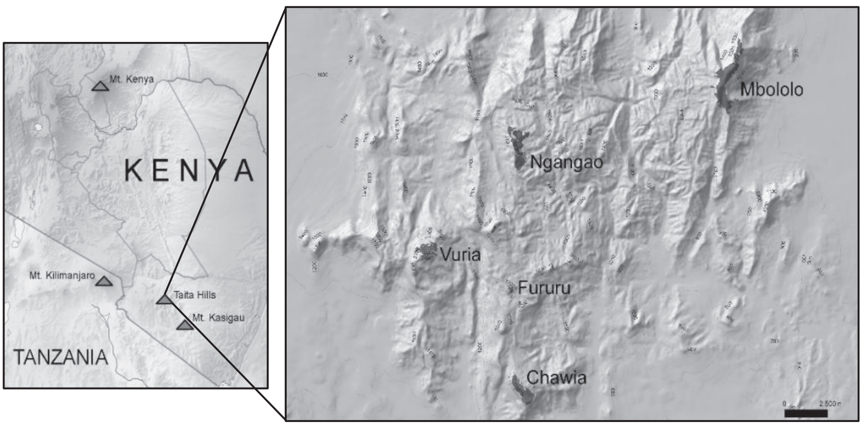

Figure 1. Geographic location of Taita Hills. Fragments of indigenous montane forests are shown in dark grey.

Table 1. Climatic differences between the study sites. Elev, elevation (m asl); Tavg, average diurnal temperature (°C); Tmin, average diurnal minimum (°C); Tmax, average diurnal maximum (°C); RHavg, average diurnal atmospheric humidity (%); RHmin, average diurnal minimum of atmospheric humidity (%); Rain, rainfall (mm). The temperature and humidity values for Vuria, Ngangao South (NG-S), and Ngangao North (NG-N) are based on iButton data collected between May 2013 and March 2014. These data should be understood to only tentatively characterize climatic conditions under the forest canopy at each site. Concurrent data from Mwanda, a weather station in open agricultural land near Vuria, are given for comparison (Source: TAITAWATER).

Site	Elev. (m asl)	T_{avg} (C°)	T_{min} (C°)	T_{max} (C°)	RH_{avg} (%)	RH_{min} (%)	Annual prec. (mm)
Mt. Vuria	2189	12.28	10.27	14.82	98.61	91.31	1283
NG-S	1856	13.97	12.12	16.24	96.99	84.97	963
NG-N	1877	14.64	12.27	18.21	93.73	78.94	943
Mwanda	1672	18.28	14.59	25.50	72.92	47.03	807

The nearly constant availability of moisture at high elevations in the Taita Hills leads to favorable growth conditions, and the moist montane forests can consequently support a rich epiphytic bryophyte flora (Enroth *et al.* 2013, 2019; Malombe *et al.* 2016). However, a vast majority of indigenous forest in the region has either been cleared for agriculture or replaced by forest plantations and secondary scrub (Pellikka *et al.* 2009; Aerts *et al.* 2010; Adhikari *et al.* 2017; Pellikka *et al.* 2018). Most remaining fragments of indigenous montane forest are small and badly degraded, which obviously threatens the existence of many forest species in the region (Brooks *et al.* 1998; Rogo & Oguge 2000; Maeda *et al.*. 2010; Malonza *et al.* 2010; Thijs *et al.* 2015; Pellikka *et al.* 2018).

Epiphyte species studied

The research data for this thesis was collected from the moist montane forests of Taita Hills in 2012–2018. For the transplant studies (Articles I & II) we chose locally common and easily identifiable epiphytes that had thallus morphologies suitable for the construction of pendent transplants. In Article I we used the mosses *Orthostichella rigida* and *Orthostichella capillicaulis* (Neckeraceae), and *Squamidium brasilience* (Meteoriaceae), the leafy liverwort *Plagiochila* sp.

(Plagiochilaceae), and the lichens *Heterodermia leucomelos* (Physciaceae) and *Usnea* sp. (Parmeliaceae). In Article II we used the mosses *Orthostichella rigida, Orthostichella capillicaulis,* and *Squamidium brasilience*.

In Article III we studied the diversity and abundance of epiphytic bryophytes and lichens that colonized fog nets placed in different types of moist montane forests and were kept there for four years. The total number of epiphytic bryophytes and lichens identified during the study was 74 (46 liverworts and 28 macrolichens).

In Article IV we reported all our collections of bryophytes from the Taita Hills (including Mount Kasigau and Maktau Hill) including all the species that established on the plastic nets studied in Article III.

Field experiments

In Article I we developed a practical method for transplanting tropical bryophyte and lichen epiphytes, and the same transplant method was also used in Article II. Young shoots of bryophytes and thalli of lichens were first collected from an upper montane forest and taken to the laboratory. They were air-dried and divided into about 0.25 g pieces; the transplant size was decided after testing different transplant sizes in a pilot study. After weighing, the biological material was wrapped in green plastic (PE) net with an aperture of 8 × 8 mm and the net tube was sealed from both ends with cable ties. A loop of fishing line was attached to the net with silicone, and the complete transplant was then weighed again to determine the weight of the rigging. We coded each rigged transplant for identification using colored plastic beads and attached the transplants to ropes according to the design of each growth experiment (Figure 2).

In addition to the rigged transplants, we also weighed several calibration specimens (ca. 0.25 g) of each epiphyte species together with the transplants and stored them dry in the laboratory. Later we weighed them together with the recovered transplants, to detect possible weight changes in the transplants due to differences in ambient air humidity. In addition, we placed empty control nets in the field together with transplants to detect possible changes in the weight of the ridding during the experiment.

In Article I, we placed a total of 558 epiphyte transplants into three different sites: one set in an upper montane cloud forest, the second set in a humid lower montane cloud forest, and the third set in a dry lower montane cloud forest. The primary data set on epiphyte growth was obtained from 324 epiphyte transplants, with the other transplants being used to study the effects of transplantation height and initial transplant weight on the performance of each epiphyte species.

Figure 2. Examples of healthy *Orthostichella rigida* transplants after three years in the field (Photos: Jouko Rikkinen).

In Article II we used three epiphytic moss species and a total of 180 pendant transplants, which were divided in three groups. For the first year the transplants were placed into the previously described forest sites, one representing the upper montane upper montane cloud forest from where the bryophyte specimens had been originally collected, and the two other sites representing warmer and drier lower montane cloud forests. For the second year, all transplants were placed into the upper montane cloud forest to document the possible recovery of those that had spent the first year under adverse climatic conditions. For the third year the remaining transplants were divided into two groups and placed into the indigenous forest and a eucalyptus plantation, both at roughly the same elevation in the upper montane zone. The experimental setup is illustrated in Figure 3.

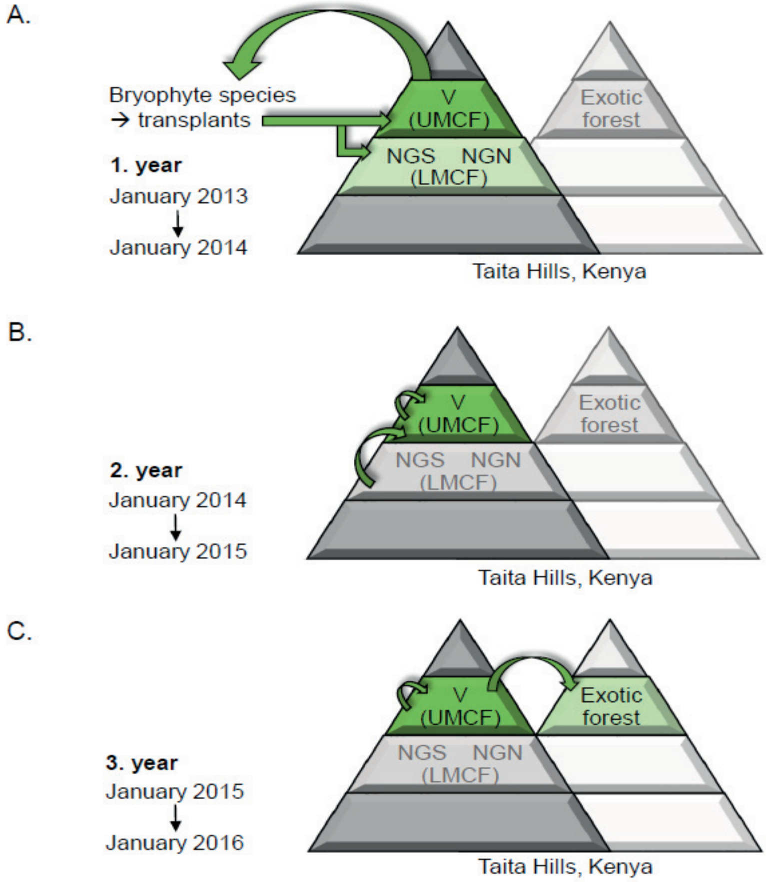

Figure 3. Experimental setup in Article II. **A.** In the first year, bryophytes were collected from the upper montane cloud forest (UMCF) on Mt. Vuria, and the transplants were prepared. The transplants were then placed at three study sites: one on Mt. Vuria (V) in UMFC, and the two other in the lower montane cloud forest (LMFC) in Ngangao South (NGS) and Ngangao North (NGN). **B.** In the second year, the transplants from NGS and NGN were returned to their original habitat on Mt. Vuria. **C.** In the third year, half of the transplants were left on Mt. Vuria, and the other half was placed in a more open and disturbed eucalyptus forest covering the neighboring secondary peak of Mt. Vuria.

In Article III we used large plastic nets (1 m^2 nets green PE net with an aperture of 8 × 8 mm) as artificial substrates to study the colonization ability of non-vascular epiphytes in different types of montane forests. The nets were initially used in open fog collectors (Räsänen *et al.* 2018) to obtain data on fog and dew deposition (October 2013 to September 2014), but were subsequently left in place to study colonization patterns of epiphytic bryophytes and lichens (Figure 4). The nets remained in place for a total of four years, after which they were taken down for analysis. In the laboratory, each net was first divided into 16 subplots (20 × 20 cm), which were cut loose, photographed and weighed. After this, the non-vascular epiphytes attached to six randomly selected subplots from each net were identified.

Figure 4. A. Fog collector in lower montane forest (Ngangao) and covered nets from upper montane forest and lower montane forest. **B.** Study sites in Ngangao. **C.** Study sites in Vuria. Photos: Jouko Rikkinen. Source of satellite images: Google Earth.

Based on our own collections and previous literature, in Article IV we reported and discussed all bryophyte species currently known from the Taita Hills region, including Mount Kasigau and Maktau Hill.

Statistical analyses

All statistical analyses were conducted using the R i386 3.5.3 (R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/) and PC-ORD 15 6.15 (McCune & Mefford 2011). We used fitted GLM with chi-square tests (Article I), mixed effects models fitted using the nlme package (Article II), and Non-metric multidimensional scaling (Article III).

4. Main results and discussion

In my first study (Article I), I developed a transplant methods for studying the growth of tropical epiphytes and the effects of the forest environment on their performance. The transplant study revealed significant differences in the performance of all studied epiphyte species among the different forest sites. In general, epiphytic bryophytes did better than epiphytic lichens, and all studied mosses either maintained or increased their biomass when transplanted into the cool and humid upper montane forest. Several species grew very well in the cool and humid upper montane forests, with some individual transplants more than doubling their biomass during only one year. Conversely, the lower canopy of lower montane forests represents a marginal habitat for all the studied epiphyte species, presumably due to the unfavorable combination of warm temperatures and insufficient light. The results of my first study demonstrated that pendant transplants can be effectively used for monitoring growth of non-vascular epiphytes in tropical montane forests, and I thus applied the same method also in my second experiment.

In the second study (Article II) I transplanted three pendant moss species from an upper montane forest to two sites in the lower montane forests and measured their responses in terms of biomass accumulation. After one year under unfavorable conditions, the transplants were moved back to the upper montane forest. The difference in growth between the transplants that spent one year in unfavorable conditions and then were returned to upper montane forest, and those left in upper montane forest for the duration of the whole study was still statistically significant after the third year, even though the transplants from lower montane forest had two years to recover in upper montane forest. Additionally, there was some notable differences on species level, which indicates that unfavorable conditions may cause long-term effects on growth for some but not all epiphytic bryophyte species. This conclusion is supported by the transplant study by Jácome *et al.* 2010, where they suggested that species communities might become more even, with a decreased dominance of individual species when exposed to lower elevations. As expected, by the end of the third year the effect of the initial conditions on growth had largely decreased with all groups growing at roughly the same rate.

Interestingly, the biomass of the transplants growing in the upper montane forest during all three years increased the most, regardless of the forest type (original *vs*. eucalyptus) during the final year. This clearly demonstrate that mature pendant bryophytes can survive and even grow well in exotic plantation forests. Therefore, their sparse presence in eucalyptus stands must be related to dispersal limitation or a lack of suitable substrate.

Transplant losses during the studies reported here were generally low, and the risk of monkeys, humans or other animals destroying transplants did not turn out to be a major issue. However, I was forced to terminate some other experiments due to excessive human disturbance (data not shown). Especially after a couple of years in the field the excessive growth of some transplants also became an issue. In the upper montane forest, some transplants grew so big that the plastic net could not support their weight as effectively as in younger transplants. I also lost isolated transplants to extreme weather (strong winds and rain). Even so, I can conclude that pendant transplants offer a useful way of investigating the performance non-vascular epiphytes in experimental setups that do not last for more than 3–4 years.

In the third study (Article III) I took another approach and focused on the dispersal and colonization of non-vascular epiphytes in the same forests where the transplant studies were made. My approach was again experimental, but now polyethylene nets were placed in the field for four years, and epiphyte colonization on them analyzed. The results from this study confirmed that plastic nets can be effectively used to study colonization of non-vascular epiphytes. We found out that in the upper montane forest liverworts effectively colonized nets underneath the forest canopy, whereas lichens became dominant on the nets placed in open areas. In the drier lower montane forest epiphyte cover, biomass and epiphyte diversity were relatively low and especially the nets of open sites became mainly covered with algae and crustose lichens. We concluded that light and atmospheric moisture were highly important factors in understanding the dispersal of non-vascular epiphytes. Interestingly, not a single epiphytic moss species was able to colonize any of the plastic nets in four years, despite being abundantly present especially in the upper montane forest (Stam *et al.* 2017). We suspect that these pendant bryophytes primarily disperse as relatively large fragments, which do not easily attach to vertical plastic nets.

Due to local climatic changes and desiccation some species of non-vascular epiphytes in East-Africa may be facing regional or even global extinction (Gradstein 1992; Zotz & Bader 2009; Metcalfe & Ahlstrand 2019). Results from temperate forest ecosystems have shown that some epiphyte communities can respond to environmental change abruptly, but their recovery may take hundreds of years (Chapman & King 1983; Root *et al.* 2014; Scheidegger & Werth 2009). It remains largely unknown how fast epiphytic bryophytes and lichens can recover and re-establish in tropical ecosystems when they have disappeared from the regional species pool. Obviously, epiphyte richness also varies considerably between different forest types and it is therefore dangerous to generalize the recovery speed (Gradstein 1992).

In the fourth study (Article IV) we produced an annotated checklist of bryophytes, including all epiphytic species for the Taita Hills region. This was done partly to establish a solid basis for future work and to take the first step towards elucidating the bryophyte taxa that are likely to be most strongly hit by climate change.

On the basis of this work, and additional unpublished data (Fig. 5), we fear that all non-vascular epiphyte species that have so far been only found from habitats above 1900 m asl in the Taita Hills are in great danger of going regionally extinct if global warming and associated drying proceeds as predicted (IPCC 2018). A list of such bryophyte species in provided in Table 2, recognizing that the list is almost certainly incomplete as many rare species probably remain unrecognized.

A similar list on epiphytic lichens cannot yet be produced due to poor overall knowledge of the local lichen flora. Unfortunately, we are only in the beginning of understanding the potential effect of drought on the local non-vascular epiphytes and our list can only give a preliminary idea of the potentially most threatened species in the region. In this respect, the montane forests of Taita Hills do not differ from other TMCF:s in which climate change and the introduction of exotic species are serious threats to indigenous biodiversity (Zotz & Bader 2009, Gómez González *et al.* 2017).

The number of professionals and amateurs interested in non-vascular epiphytes and with the skills required for identifying them to any meaningful taxonomical level is extremely limited when compared to those who study vascular plants (Hedenäs *et al.* 2002; Gignac 2011; Zotz 2013). One of the main purposes of my study was to develop simple research tools and thus promote study these important organisms in some of the most fragile, yet unique, ecosystems in the world. The same reasoning supported the assessment of all previously existing knowledge and new findings into a regional check-list for the benefit of the wider research community.

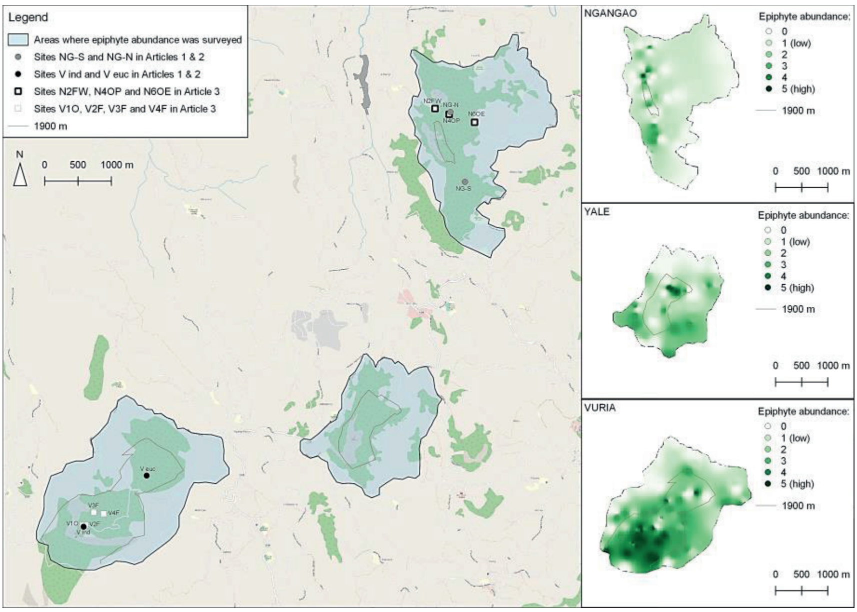

Figure 5. Highest peaks of Taita Hills surveyed for non-vascular epiphyte abundance and the diversity of dominant moss species (Stam *et al.*, unpubl.). The study sites of Articles I–III are also shown. The green shading indicate predicted (QGIS 3.6.2., algorithm Inverse Distance to Power) abundance of non-vascular epiphytes on the highest elevations (> 1900 m, shown by brown contour) of each peak.

Table 2. Preliminary list of epiphytic bryophytes most threatened by climatic warming in the Taita Hills. These taxa have only been reported from elevations above 1900m asl. (Enroth *et al.* 2019).

Epiphyte taxa	Vuria	Yale	Ngangao
Aerobryopsis capensis	+	-	-
Aerolindigia capillacea	+	+	-
Barbella capillicaulis var. *capillicaulis*	+	-	-
Campylopus nanophyllus	-	+	-
Hypnum cupressiforme	+	-	-
Porotrichodendron madagassum	+	-	-
Porotrichum elongatum	+	-	-
Porotrichum stipidatum	+	-	-
Pterobryopsis hoehnelii	+	-	-
Rhynchostegiella sp.	+	-	-
Rhynchostegium comorae	+	-	-
Rhynchostegium sp.	+	-	-
Rigodium toxarion var. *toxarion*	+	-	-
Sematophyllum sp.	+	+	-
Squamidium brasiliense	+	-	-

To conclude, transplant experiments offer a useful way of studying various environmental factors that affect the distribution of non-vascular epiphytes (e.g. McCune *et al.* 1996; Jácome *et al.* 2011; Song *et al.* 2012). Before my studies these methods had rarely been applied in studies of tropical epiphytes, despite the increasing recognition of their ecological importance (Zotz *et al.* 2010; Gignac 2011; Metcalfe & Ahlstrand 2019). By relocating epiphytic mosses and lichens, one can gain information on how these organisms are likely to respond to ongoing global warming, and of their capacity of resilience and recovery. The impact of climate change on epiphyte communities is a timely topic, especially given the importance of epiphyte communities in local water and nutrient cycling and their role as important resources for insect and animal communities (Gradstein 1992; Zotz *et al.* 2010; Slack, 2011). One must also emphasize that, due to their very intimate relationship with the surrounding atmosphere, non-vascular epiphytes can potentially be used as bio-indicators before their growth environment is more widely affected by climate change (Gignac 2011).

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